EARLY MISSISSIPPIAN HYOLITHA FROM NORTHERN IOWA

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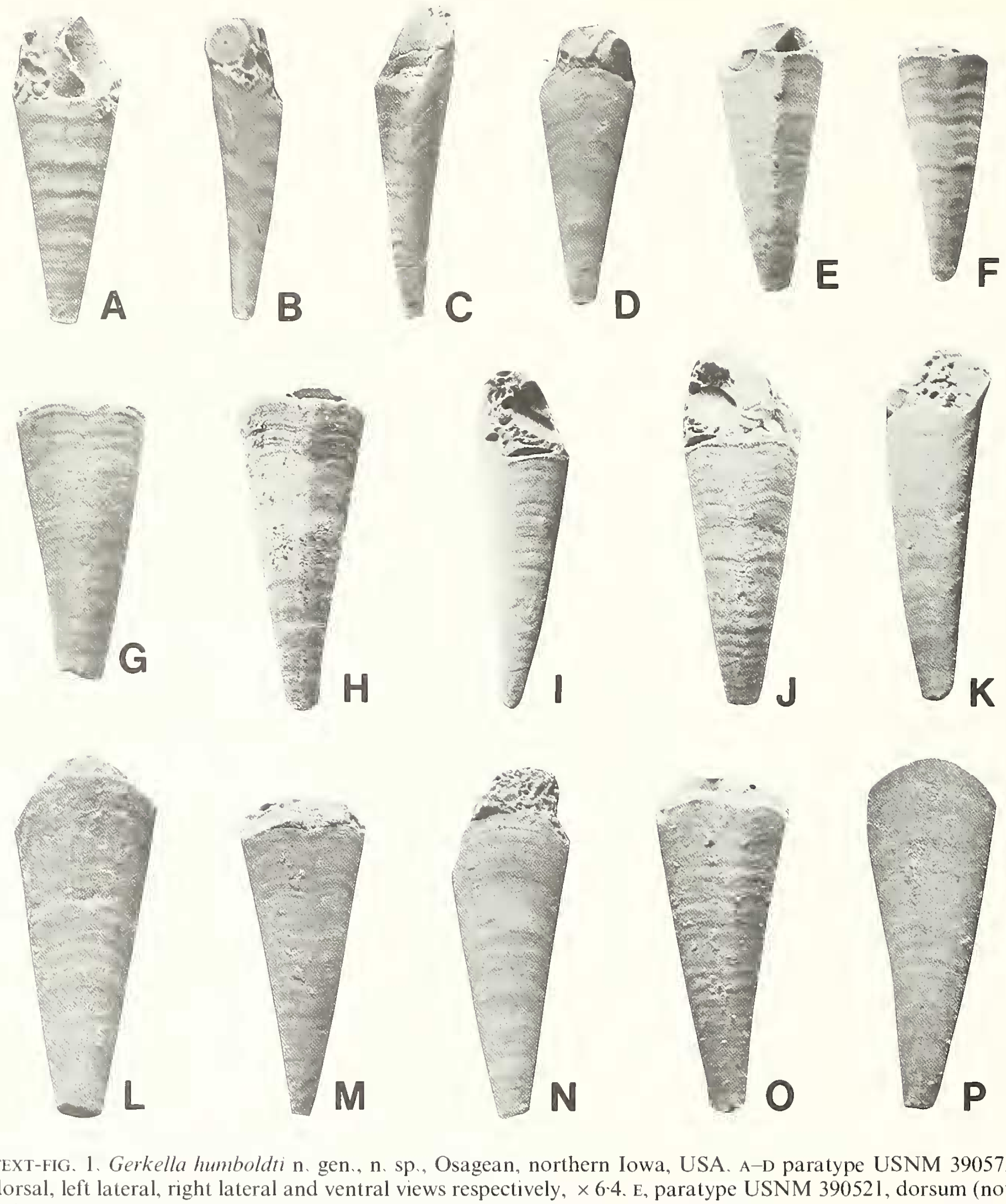
ABSTRACT. The exceptionally fine preservation and large number of specimens from a single late Palaeozoic locality makes the hyoliths in the Humboldt Oolite (Osagean, lower Mississippian) unique. All specimens are assigned to *Gerkella humboldti* n. gen., n. sp., family Hyolithidae, order Hyolithida. There is considerable variation in certain morphological features, such as transverse shape, nature of ornament and apical curvature; however, these differences are judged to be gradational. This indicates that certain features may be variable within one species and shows that establishment of hyolith species should be based upon a variety of features. Other North American late Palaeozoic hyoliths include *Hyolithes carbonaria* Walcott, *H. milleri* Sinclair, *H. parvulus* Girty and *H. waverliensis* Hyde. Their types lack important morphological features, which makes their generic identifications uncertain. Their names should not be used for any further material until better preserved topotypes become available for study.

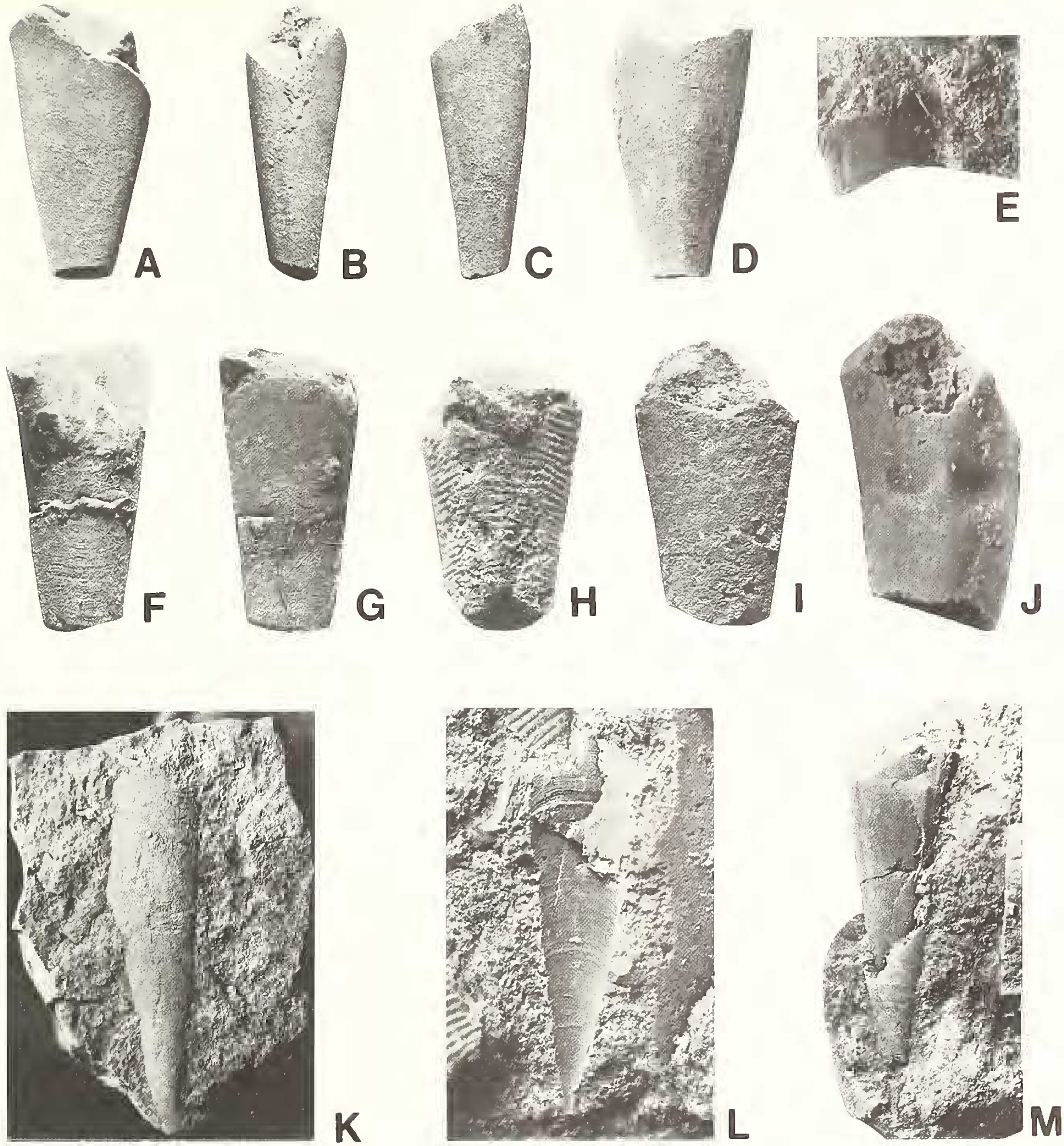
EARLY Palaeozoic hyoliths are currently under intensive investigation in the Soviet Union, China and North America. However, late Palaeozoic hyoliths have received much less attention largely because of rare occurrence. Only six late Palaeozoic species, represented by fewer than ten specimens, have been reported in North America since the mid-nineteenth century (Sinclair 1946). The number of late Palaeozoic specimens drastically increased with the discovery of approximately forty specimens from the Missourian (Pennsylvanian) Eudora Shale of southeastern Kansas (Malinky and Mapes 1983) and more than 1000 specimens from the Pennsylvanian of Kansas, Oklahoma and Texas (Malinky *et al.* 1986). Unfortunately, only a small number of those specimens can be identified to genus; most are poorly preserved steinkerns and cannot be assigned to genus or species. Therefore the discovery of seventy-six well preserved hyoliths from the lower Mississippian of northern Iowa is unique among late Palaeozoic occurrences because of the large number of exceptionally well preserved specimens from one late Palaeozoic locality. Morphology of these specimens indicates that all represent the same species; they are assigned to *Gerkella humboldti* n. gen., n. sp., in the family Hyolithidae and order Hyolithida (text-fig. 1A–P).

Finding these specimens permits a survey of the range of morphological variation within a hyolith species. This further allows assessment of the taxonomic significance of features such as transverse shape and curvature of the apical end of the shell. Transverse shape in particular was used as the ruling criterion for establishing hyolith species in the nineteenth and early twentieth century (Barrande 1867; Novak 1891; Holm 1893; Walcott 1886, 1889, 1890; Resser 1938). It formerly served as the sole distinguishing feature between *Hyolithes* Eichwald, 1840, and *Orthotheca* Novak, 1886, the only two generic names in use for hyoliths until recently (Syssoiev 1958, and many other Soviet and Chinese publications). These genera now form the basis for the orders Hyolithida Matthew *fide* Fisher, 1962, and Orthothecida Marek, 1966, within the class Hyolitha Marek, 1963. Recent studies by Marek (1963, 1967) suggested that while transverse shape remains a characteristic to be considered for diagnosis and recognition of hyolith taxa, other features of the conch and operculum must also be used when available. The gradational nature of transverse shape and other morphological features, such as prominence of growth lirae on the shell, indicates that all specimens from the Humboldt Oolite belong to one species.

In addition to *G. humboldti*, other North American late Palaeozoic hyoliths are the Mississippian species *Hyolithes aculeatus* (Hall, 1860) from Indiana, *H. milleri* Sinclair, 1946 from Missouri, *H.*



TEXT-FIG. 1. *Gerkella humboldti* n. gen., n. sp., Osagean, northern Iowa, USA. A–D paratype USNM 390573, dorsal, left lateral, right lateral and ventral views respectively, ×6·4. E, paratype USNM 390521, dorsum (note apical curvature toward right), ×7·4. F, paratype USNM 390554, dorsum (note apical curvature toward left), ×6·3. G, paratype USNM 390543, dorsum (note apical curvature toward left), ×7·2. H, paratype 390532, dorsum (note curvature toward right), ×8·3. I, J, N, holotype USNM 390504, left lateral, dorsal and ventral views respectively, ×4·5. K, L, paratype USNM 390531, left lateral and ventral views respectively, ×5·7. M, paratype USNM 390552, dorsum, ×7·5. O, P, paratype USNM 390545, dorsal and ventral views respectively, ×5·8.



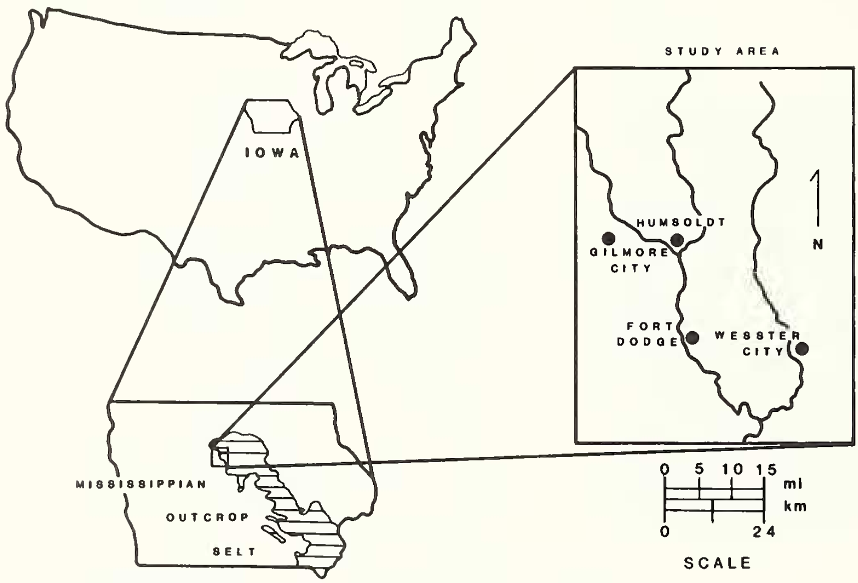
TEXT-FIG. 2. A–D, *Hyolithes waverliensis* Hyde, holotype OSU 19895, ventral, right lateral, left lateral and dorsal views respectively, × 5·3. E, J, L, M, *H. carbonaria* Walcott, USNM 14426. E, shell at anterior edge of ligula, × 5. J, internal mould of dorsum, × 8. K, external mould of venter, × 10. L, internal mould of venter with some shell near apical end, × 10. F–I, *H. parvulus* Girty. F, G, lectotype USNM 121196, dorsum and venter respectively, × 7·2. H, I, paralectotype USNM 122195, dorsum and venter respectively, × 7·5. K, *H. milleri* Sinclair, lectotype UCGM 3900A, venter, × 2.

parvulus Girty, 1926 from Texas and *H. waverliensis* Hyde, 1953 from Ohio, and the Pennsylvanian species *H. carbonaria* Walcott, 1884 from Nevada (text-fig. 2A–M). The types of *H. carbonaria*, *H. milleri*, *H. parvulus* and *H. waverliensis* are incomplete, hence their generic identifications may be doubted. The names of these species should not be used for any further material until better-preserved topotypes become available for study. The type or types of *H. aculeatus* (Hall, 1860) cannot be located at present; however, the published description of that species indicates that few morphological features are preserved, so that its generic identification is uncertain.

Three other Carboniferous species, *H. roemeri* Koenen, 1879, *H. sicala* Koninck, 1883 and *H. sturi* Klebelsberg, 1912 were reported from western Europe. Although these specimens have not been examined, published descriptions and illustrations of the types indicate that preservation is poor, again rendering generic identifications doubtful. Preservation of more recently-discovered specimens considered to be hypotypes of those species (Zakowa 1971) from the *Goniatites granosus* zone of eastern Europe is not sufficiently good confidently to identify those specimens.

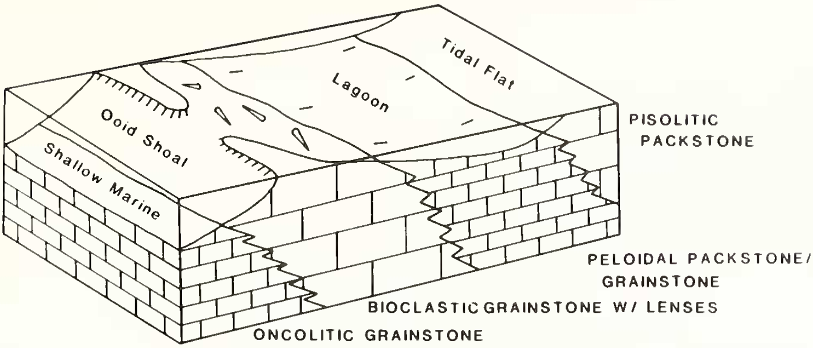
PALAEOECOLOGY AND MORPHOLOGICAL VARIATION

Stratigraphic setting and palaeoenvironment. G. humboldti was discovered in the Osagean (Early Mississippian) Humboldt Oolite near Humbolt in northern Iowa (text-fig. 3). The palaeoenvironment of this unit was studied in detail by Gerk and Levorson (1982) and Glenister and Sixt (1982); detailed stratigraphic sections of that locality showing distribution of fauna were given by Glenister and Sixt (1982) and by Brenkle and Groves (1985). Previous studies of fauna were summarized by Glenister and Sixt (1982). More recent taxonomic studies of the trilobites and foraminiferans are those of Brenkle and Groves (1985) and Brezenski (1988) respectively. The hyoliths described herein were only previously mentioned once in an unpublished study of the gastropods of this unit (Harper 1977).



TEXT-FIG. 3. Locality map of *Gerkella humboldti* n. gen., n. sp.

The hyoliths occur within the bioclastic grainstone facies of the Humboldt Oolite (text-fig. 4). That facies includes a series of poorly-indurated, friable, ooid grainstone lenses, 50–200 mm thick which are most common near the middle of the section. The lenses also contain abundant, small, apparently size-sorted gastropods, brachiopods, bivalves, rostroconchs, ostracods and calcareous algae, all of which are exquisitely preserved. According to Gerk and Levorson (1982), the Humboldt Oolite is thought to represent a shallow to marginal marine deposit which originated in an arid climate. More normal marine deposits occur at the base of the section with environmental and facies



TEXT-FIG. 4. Reconstruction of facies during deposition of Humboldt Oolite. Hyolith shells (◅) accumulated in lenses on bars or shoals (bioclastic grainstone) which sheltered a lagoon (peloidal packstone/grainstone).

restriction progressively increasing toward the top. The bioclastic grainstone represents a series of bars or shoals that sheltered a lagoon in which the sparcely fossiliferous peloidal packstone facies originated. Gerk and Levorson (1982) suggested an analogy between the hyolith-bearing lenses and recent shell beds in protected back-beach areas of the Bahamas. These modern shell deposits resemble the Humboldt lenses in size, lithofacies association and faunal diversity. The Bahamian deposits are thought to have originated from a coincidence of high tide and a south-west wind, rather than from fair weather wave agitation or reworking associated with storms. Movement of water at high tide transports shells to back-beach areas where they are protected from further reworking. Under these circumstances chances of preservation are greater. Conditions resulting in such deposits are unusual and occur only several times a year. A similar origin was suggested by Gerk and Levorson (1982) for the lenses in the Humboldt Oolite.

Hyolith palaeoecology and taphonomy. Various aspects of hyolith palaeoecology were summarized by Fisher (1962) and by Marek and Yochelson (1964, 1976) and will not be reviewed in detail here. However, the unusual lithologic and environmental setting of *G. humboldti* requires additional comment. Because the hyoliths are relatively small they cannot be observed directly on outcrop and their distribution and orientation within the matrix are unknown. None the less, some generalizations on the palaeoecology and taphonomy of this species are still possible.

Late Palaeozoic hyoliths in North America occur in a wide variety of facies from shallow normal marine to offshore, oxygen-poor facies, however they only seem to be abundant in facies which originated in stress environments. Hyoliths have been discovered in normal marine facies such as sandstone (*H. waverliensis* Hyde, 1953 from Ohio), shale (Malinky, unpublished data), and limestone (all remaining Mississippian occurrences and the Pennsylvanian *H. carbonaria* Walcott, 1884). This indicates that they were widespread in the marine environment despite their relatively low abundance at any single locality. However, the taxa from normal marine environments are represented by only one or two individuals each. In contrast, in late Palaeozoic facies from stress environments assemblages of hundreds of hyoliths are known. More than 1000 specimens from fourteen different shale units have been discovered in offshore marine though oxygen-poor shales (Heckel 1977) from the Pennsylvanian of the southern Midcontinent (Malinky *et al.* 1986). Kammer *et al.* (1986) suggested that this type of environment served as a refuge for hyoliths and other 'archaic' taxa such as monoplacophorans which were abundant in the lower Palaeozoic but uncommon in middle and upper Palaeozoic strata. In the oxygen-stressed Pennsylvanian marine environment dysaerobic conditions would have excluded all benthos except those forms such as the hyoliths which seem to have been specially adapted to it. The relative scarcity of other organisms owing to oxygen stress would have decreased competition with the mechanically inefficient hyoliths (Yochelson 1984).

The environment represented by the Humboldt Oolite includes a number of microenvironments, and therefore it is heterogenous or 'coarse-grained' (Ricklefs 1979) for slightly mobile, benthic organisms with regard to water depth, amount of agitation and suspended sediment in the water, and salinity fluctuation. Because the bioclastic grainstone facies was deposited nearshore, environmental stress during deposition would have been caused by these factors rather than by low oxygen. Most stenotopic organisms would have been excluded from an environment such as this except for those specially adapted to it. Even though *G. humboldti* may not have lived in the lenses where it was discovered, the fine preservation of specimens indicates that the amount of transport was minimal and that this form was without question a shallow marine, nearshore species. The relative abundance of this species in the Humboldt Oolite (compared to other Mississippian units) suggests that the species was well adapted and even opportunistic in this particular environment. Yet compared to other invertebrates normally seen in late Palaeozoic marine strata, hyoliths constitute only a small portion of the fauna in the Humboldt Oolite.

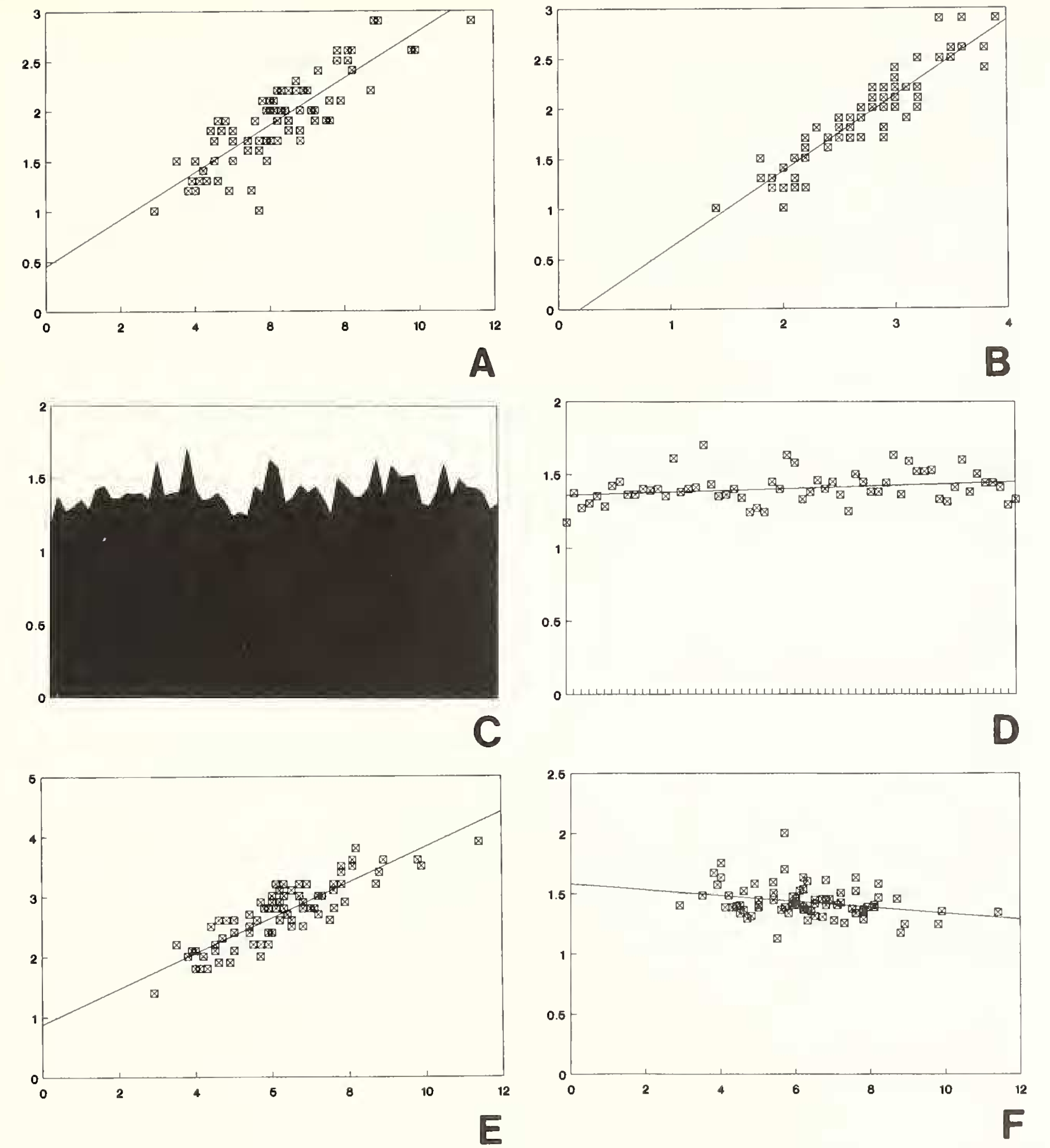
All ontogenetic stages seem to be represented among the Humboldt hyoliths although the larger, and presumably adult, individuals seem to predominate. This may be partly a function of winnowing in which smaller individuals were removed, or it may reflect normal mortality within a breeding population. Individuals dying in old age will normally disarticulate, and the operculum and helens may be lost. Hyoliths buried alive by a sudden influx of sediment might be articulated (Yochelson, pers. comm. 1984). Most of the hyoliths in the Humboldt Oolite may have died from old age, although if any were rapidly buried while alive, winnowing has caused disarticulation of hard parts for those individuals as well.

Following burial, the hyolith conchs in the Humboldt Oolite filled with sediment and small skeletal debris. The sediment and the shells neomorphosed into blocky calcite spar causing all traces of original shell structure to be destroyed. The boundary between the inner shell wall and the spar is distinct, but it is impossible to separate the two to search for muscle scars or other features on the interior of the shell. Calcite spar readily separates from the outer shell wall, suggesting some microenvironmental differences in diagenetic conditions between the interior and exterior of the shell. Lack of oncolitic coatings on the hyoliths suggests either sufficient turbidity to block out sunlight or rapid burial of shells following winnowing.

Morphological variation. Morphological criteria by which species may be recognized among hyoliths were listed by Syssoiev (1958) and Marek (1967). They specifically mentioned: length of shell (L), shell thickness, width (W) and height (H) of aperture, details of growth lirae and other ornament, apical curvature, and various angular measurements of the aperture and apex. Marek (1967) also listed many features of the operculum, but these are not considered here because the operculum of *G. humboldti* is unknown at present. Based upon the number of specimens used by these authors in naming new taxa, neither Marek nor Syssoiev had access to as many individuals as are used in this study. Presumably for these authors, morphological gaps existed between specimens from different horizons or different localities, thereby suggesting taxonomic status.

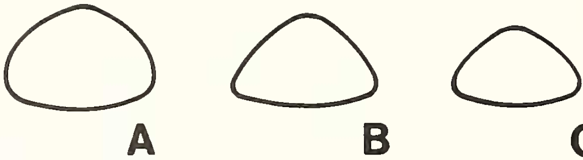
The hypothesis proposed herein is that all hyoliths from the Humboldt Oolite represent the same species. They occur at the same stratigraphic position and in the same facies, but by themselves these criteria are not conclusive. An examination of selected morphological features must be undertaken either to separate specimens into discrete species, or to survey the range of variation among selected features within the same species. The criteria selected to test the species hypothesis are length of shell, apical curvature, and width and height of the aperture (= transverse shape). These features were chosen specifically because they allow accurate measurement. Other features, such as length of the ventral ligula and nature of growth lirae cannot be used with the same degree of certainty as the features listed above. On many of the Humboldt specimens the ligula is incomplete and variation among growth lirae may reflect partial dissolution of the outer shell wall. Apical and lateral angles are not used because they are directly proportional to the width and height of the aperture, and their distribution will follow that of the apertural parameters.

Bivariate plots of the apertural characteristics and a visual comparison of apical curvature



TEXT-FIG. 5. A, apertural width (W) plotted against apertural height (H). B, H plotted against length of shell (L). C, distribution of W/H among Humboldt hyoliths. D, trend in W versus H. E, H plotted against L. F, L plotted against W/H. Absence of clusters among points demonstrates that, based upon these selected characteristics of the shell, all specimens studied herein belong to the same species.

strongly support the notion that all Humboldt hyoliths belong to the same species (text-fig. 5). These results suggest that caution should be used when erecting hyolith taxa based upon relatively few characteristics. Even at present, transverse shape remains the major criterion for some workers when naming and recognizing hyolith species (Syssoiev 1962, 1968; Landing 1988; and many others). Had only the specimens from each end of the range of variation been discovered, the case for more than one species based upon transverse shape would have been strong because of the large morphological gap between specimens (text-fig. 6). Conversely, different species established on features such as growth lirae or apertural morphology including lateral sinuses or an apertural flare may have similar transverse shapes. In this case, the large population of hyoliths demonstrates that the selected characteristics are gradational among specimens, although the amount of variation seen here may not be typical of all hyolith populations. The adaptive significance in this environment, if any, for the characteristics mentioned above is unknown.



TEXT-FIG. 6. Transverse sections of *Gerkella humboldti* n. gen., n. sp. A, holotype USNM 390504. B, paratype USNM 390521. C, paratype USNM 390545. All ×10.

SYSTEMATIC PALAEONTOLOGY

Class HYOLITHA Marek, 1963
Order HYOLITHIDA Matthew *fide* Fisher, 1962
Family HYOLITHIDAE Nicholson *fide* Fisher, 1962

Genus GERKELLA gen. nov.

Etymology. The genus is named in honour of Arthur J. Gerk, who discovered these specimens.

Type species. *Gerkella humboldti* n. gen., n. sp.

Diagnosis. Hyolithid which has rugae on the exterior of the shell. Apertural rim is orthogonal without a flare, and the ligula is short.

Included species. *G. humboldti* n. sp. and possibly *H? centennialis* (Barrett, 1876) from the Devonian of New York.

Remarks. This genus is distinguished from others included under the Family Hyolithidae (see Malinky 1988 for list of genera) by the presence of rugae on the shell and other details of ornament and apertural characteristics. *Hyolithes* Eichwald, 1840, *Carinolithes* Syssoiev, 1958, *Sololites* Marek, 1967, *Maxilites* Marek, 1972, *Cavernolites* Marek, 1974, *Nervolites* Marek, 1974, and *Dilytes* Marek, 1974 possess longitudinal sculpture on the shell which *Gerkella* lacks. In addition, *Eumorpholites* Marek, 1967, *Lirotheca* Malinky and Mapes, 1983, and *Darwinites* Malinky, Mapes and Broadhead, 1986 possess a distinct apertural flare which *Gerkella* lacks. *Elegantilites* Marek, 1967, and *Joachimilites* Marek, 1967 have a small apical angle and fine, closely spaced, transverse ribs which anastomoze in some places; *Gompholites* Marek, 1966, and *Buchavilites* Marek, 1975 have a tubular shell with a rounded transverse section. *Nevadotheca* Malinky, 1988 has nearly angular lateral margins and inflated slopes on the dorsum which *Gerkella* lacks.

Hyolithes? *centennialis* Barrett, 1876, from the Devonian of New York may represent this genus; the types of that species are covered with prominent rugae, making it the only recorded species from the middle Palaeozoic of North America to have rugae. The generic identification of this species is uncertain (Malinky, Linsley and Yochelson 1987) because the venter is unknown. Until complete specimens become available for study, that species is tentatively retained under *Hyolithes*.

Stratigraphic range. ?Middle Devonian; Osagean, Lower Mississippian.

Gerkella humboldti n. sp.

Text-fig. 1A–P

Etymology. The species is named after the locality where it was discovered.

Diagnosis. *Gerkella* which has a shallow sinus along the apertural rim of the dorsum.

Description. The shell of this species has a broad, nearly flat to slightly inflated venter, which grades into narrowly rounded lateral margins. The dorsum is inflated with a narrowly rounded longitudinal axis and the adjacent slopes vary from nearly flat to slightly inflated. The ligula along the ventral apertural margin is short, and the anterior edge is straight. The dorsal apertural rim lacks a flare, but a shallow sinus occurs in the rim along each lateral margin and in the middle of the dorsum. The apertural rim is orthogonal (perpendicular to the venter). The apical angle of the shell is small, and the apical end curves either to the left or right when viewed dorsally, and on some specimens it also curves toward the venter. The transverse section of the shell is subtriangular (text-fig. 6).

The exterior of the shell is covered with widely spaced rugae. On the venter, the rugae curve to follow the outline of the anterior edge of the ligula. The rugae curve on the lateral margins to form a shallow sinus, parallel to that in the apertural rim, and on the dorsum the rugae are nearly transverse except for a shallow median sinus which follows that of the apertural rim. The operculum and helens are unknown.

Remarks. This species is currently known from seventy-six specimens; specimen USNM 390504 is selected as holotype because it is the most complete and best preserved. That specimen is 8·8 mm long, and has an apertural width and height of 2·6 mm and 2·3 mm respectively. Neither the holotype nor any paratype is operculate, and no disarticulated opercula or helens have been found for this species. All specimens are free of matrix, although the interiors of the shells contain blocky calcite spar which cannot be removed without destroying the specimens. Details of the interior are unknown.

The specimens upon which this species is based were collected over a twenty year period by A. J. Gerk of Mason City, Iowa. These hyoliths were mentioned in a study of the Gastropoda of the Humboldt Oolite by Harper (1977), who regarded them as conspecific with *Hyolithes*? *waverliensis* Hyde, 1953 from the Mississippian of Ohio. That species is based upon a steinkern which lacks most taxonomically important characteristics such as all features of the apertural end. No meaningful comparison between that species and *G. humboldti* is possible, and the two are herein treated as separate species.

Material. Holotype USNM 390504 and seventy-five paratypes under 390505 through 390580.

Occurrence. P. & M. Hodges quarry, sec. 32, T92N, R28W, northeast of Humboldt, Humboldt County, north-central Iowa, from the Humboldt Oolite, Osagean (lower Mississippian) (text-fig. 3).

Stratigraphic range. Osagean.

Class HYOLITHA *incertae sedis*

Hyolithes? *aculeatus* (Hall, 1860)

1860 *Pugiunculus*? (*Theca*) *aculeatus* Hall, p. 107.
1862 *Pugiunculus*? *aculeatus* Hall; Winchell, p. 423.
1865 *Pugiunculus*? *aculeatus* Hall; Winchell, p. 131.
1898 *Hyolithes aculeatus* (Hall); Weller, p. 311.
1946 *Hyolithes aculeatus* (Hall); Sinclair, p. 73.
1967 *Hyolithes aculeatus* (Hall); Yochelson and Saunders, p. 9.

Description. 'Elongate, obtusely triangular bodies, having one side nearly flat, and the other two sides meeting at a very obtuse angle, and slightly incurved towards the angle, the flat side being convex in the direction of the length. Aperture obtusely triangular, and a little thickened on the straight side of the lateral angles' (Hall 1860, p. 107).

Remarks. This species was named and described but not illustrated by Hall (1860, p. 107). To date, this species apparently has never been illustrated, yet the name has been used for other specimens by later workers (see below). Hall (1860) did not select a holotype for this species, and the type or types cannot be located at present. Hall's description, and indeed, the fact that he was uncertain of the generic identification, leaves little doubt that preservation of the type material was poor. Because so few characteristics of this species are known, its name should not be used for any additional specimens.

Winchell (1862, 1865) referred hyoliths which he described as casts 'without external markings' to *P.? aculeatus*, but he provided no additional details of those specimens or their occurrences. Weller (1898), Sinclair (1946) and Yochelson and Saunders (1967) listed the species name in their respective compilations of hyolith species without reporting any specific occurrences other than that of the type. Weller (1898) listed the species under *Hyolithes* because by that time, both *Pugiunculus* Barrande (1847), and *Theca* (Sowerby *fide* Morris 1845) were regarded as junior synonyms of *Hyolithes*.

Occurrence. Hall (1860, p. 107) discovered this species in the 'Goniatite limestone near Rockford, Indiana.' That unit is now called the Rockford Limestone (lower Mississippian, Osagean; Gray 1979). Winchell's (1865) specimens were discovered in the Marshall Formation (Osagean; Ellis 1979) in the SE 1/2 SW 1/2 sec. 23, Adam, Hillsdale County, Michigan and in 'Alan's and Germain's quarries, Hillsdale,' Michigan (Winchell 1862).

Hyolithes? *carbonaria* Walcott, 1884

Text-fig. 2E, J, L, M

v* 1884 *Hyolithes carbonaria* Walcott, p. 264, pl. 23, fig. 3.
v* 1892 *Hyolithes carbonaria* Walcott, p. 333.
v* 1946 *Hyolithes carbonaria* Walcott; Sinclair, p. 74.
v* 1967 *Hyolithes carbonaria* Walcott; Yochelson and Saunders, p. 9.

Description. The venter of this species is flat, but curves slightly to grade into narrowly rounded lateral margins. The dorsum is low, and the longitudinal axis is narrowly rounded. The slopes adjacent to the axis are nearly flat. The ligula along the ventral apertural margin seems to be short, and the anterior edge appears to have been flat. The ligula appears to curve slightly toward the venter.

The shell on the venter is covered with fine, closely-spaced lirae which follow the outline of the anterior edge of the ligula. Two longitudinal sulci are located at each edge of the venter and they extend for the entire length of the venter. The sulci are prominent near the apertural end, but become shallower toward the apical end. The dorsal internal mould is smooth except for a prominent indentation located near the apertural end on each slope. The operculum, the shell on the dorsum and the complete aperture are unknown.

Remarks. The holotype and only known specimen of this species is 9·5 mm long, and has an apertural width of 2·3 mm. The holotype exists as several counterparts; an external mould furnishes details of the venter, a portion of the internal mold provides some detail of both dorsum and venter, and a fragment of internal mould with shell embedded in matrix furnishes further details of the venter and interior of the shell. Unfortunately, the dorsal apertural rim and the shell on the dorsum are unknown. This specimen lacks an operculum, and no disarticulated opercula were included in this species.

The indentations on the dorsal internal mould resemble those of *Lirotheca wilsoni* Malinky and Mapes, 1983, from the Pennsylvanian of Kansas. *Maxilites maximus* (Barrande, 1867) from the Caradocian of Czechoslovakia also has two crescent-shaped indentations on the dorsum which may represent muscle scars (Marek 1967), but these are smaller and narrower than the indentations on *H. carbonaria*. Walcott (1884) also compared this species to *H. aclis* Hall, 1876, from the Devonian of New York, but the apertural rim on that form is flared, whereas the apertural rim of *H. carbonaria* is unknown.

Material. Holotype USNM 14426, National Museum of Natural History.

Occurrence. Walcott (1884, p. 264) reported that this species was discovered in the 'Lower portion of the Lower Carboniferous limestone, in canon directly south of a small conical hill on the east side of Secret-canon-road Canon, Eureka District, Nevada.' This locality is probably in the NW 1/4, SE 1/4, sec. 36, T19N, R53E, Pinto Summit (15 minute) quadrangle. The 'Lower Carboniferous' limestone is probably the Ely Limestone, now recognized as Morrowan (early Pennsylvanian) in age (Larson and Langenheim 1979).

Hyolithes? *milleri* Sinclair, 1946

Text-fig. 2K

v* 1894 *Hyolithes lanceolatus* Miller, p. 317, pl. 19, figs. 35, 36.
v* 1946 *Hyolithes milleri* Miller; Sinclair, p. 73.
v* 1967 *Hyolithes milleri* Miller; Yochelson and Saunders, p. 9.
non 1845 *Hyolithes lanceolatus* Morris, p. 289, pl. 18, fig. 8.

Description. The conch of this species has a small apical angle, and the apical end appears to be straight. The venter is nearly flat, and that side is smooth without any lirae or other ornament. The ligula is short and the anterior edge appears to be straight. All other features, such as the aperture and operculum are unknown.

Remarks. Characteristics attributed to this species by Miller (1894) were derived in part from about two dozen phosphatic tubes which Miller (1894) mistakenly included under this species. *H. milleri* is unequivocally represented by one specimen (UGGM 3900A) and possibly by a second (UCGM 3900B); the phosphatic tubes were transferred to *Enchostoma* by Miller and Gurley (1896). Miller's illustration of *H. milleri* is a line drawing of a phosphatic tube that bears no resemblance to any authentic hyolith. Until now, these hyoliths have never been illustrated with photographs.

Specimen UCGM 3900A is here designated the lectotype; it is 19·5 mm long, and has a width of 4·4 mm. Only the venter is exposed; the dorsum is embedded in matrix from which extraction intact would probably be impossible. Whether that specimen has a shell or is an internal mould is not known with certainty. If shell is preserved, it appears to be smooth and featureless. The presence of an operculum cannot definitely be ascertained because the apertural end is concealed by matrix. Miller (1894) named this species *lanceolatus*, but Sinclair (1946) renamed it because the name *lanceolatus* was preoccupied (Morris 1845).

Material. Lectotype UCGM 3900A and possible paralectotype under 3900B reposited at University of Cincinnati Geology Museum.
Occurrence. Miller (1894) reported that these specimens were discovered in the Chouteau Limestone (Kinderhookian, lower Mississippian, Thompson 1979) 'near Sedalia, Missouri'. No other details of the occurrence are known.

Hyolithes? *parvulus* Girty, 1926

Text-fig. 2F–I

v* 1926 *Hyolithes parvulus* Girty, p. 38, pl. 6, figs. 18a–18e, 19a–19d.
v* 1946 *Hyolithes parvulus* Girty; Sinclair, p. 79.
v* 1967 *Hyolithes parvulus* Girty; Yochelson and Saunders, p. 9.

Description. The venter of this species is nearly flat and grades into narrowly rounded lateral margins. The dorsum is high and the longitudinal axis is narrowly rounded. The apical end of the shell appears to be straight, and the apical angle seems to be small. The conch is covered with fine lirae; they are nearly transverse on the dorsum but curve on the venter to follow the outline of the ligula. The ligula is short and broadly rounded at the anterior edge. The complete aperture and operculum are unknown.

Remarks. Two specimens were assigned to this species by Girty (1926); specimen USNM 121196 is herein designated the lectotype. That specimen is 5·4 mm long, and has an apertural width and height of 2·9 mm and 2·0 mm respectively. The lectotype retains a shell although both ends are broken, so that the complete aperture, as well as the operculum are unknown. Preservation of a possible paralectotype (USNM 121195) of similar size is comparable to the lectotype although that specimen is covered with coarse ribs; whether it represents the same taxon as the lectotype is uncertain.

Material. Lectotype USNM 121196 and paralectotype USNM 121195, National Museum of Natural History.

Occurrence. Girty (1926, p. 38) reported these specimens from 'station 2623, about 5·0 km (3·0 miles) east of San Saba County courthouse' in San Saba County, Texas. The labels associated with the specimens give more information: 'on the SW side of the road to Chappel, about 3 miles SE of San Saba courthouse, at first sharp turn well uphill.' The unit which yielded the hyoliths is 'a thin limestone above the Ellenburger and below the Barnett Shale': this is the Chappel Limestone of late Kinderhookian to early Osagean (early Mississippian) age (Kier *et al.* 1979). A recent visit to that locality by J. M. M. showed that the limestone remains exposed on the southwest side of Chappel Road, but no additional hyolith material was discovered.

Hyolithes? *waverliensis* Hyde, 1953

Text-fig. 2A–D

v* 1953 *Hyolithes waverliensis* Hyde, p. 335, pl. 53, figs. 10–15.
v* 1967 *Hyolithes waverliensis* Yochelson and Saunders, p. 9.

Description. The conch of this species has a broadly rounded venter which grades into narrowly rounded lateral margins. The dorsum is low and narrowly rounded along the longitudinal axis; the adjacent slopes are slightly inflated. The apical angle is small, and the apical end curves slightly toward the dorsum.

The lateral margins of the internal mould are covered with faint transverse growth lirae, and along each lateral margin faint longitudinal lirae are present. The shell, complete aperture and operculum are unknown.

Remarks. This species is known from a steinkern and a fragmentary external mould, both of which are counterparts of the holotype. The steinkern is 8·0 mm long, and has an apertural width and height of 5·0 mm and 3·0 mm respectively. Both ends of the steinkern are broken, and no apertural detail is preserved. The steinkern has no operculum, and no disarticulated opercula have been identified for this species.

The appearance of the steinkern closely matches the line drawings of figures 13 and 14 on plate 53 (Hyde 1953); figures 10–12 on that plate seem to be restorations for no available specimens of this species match those illustrations, and there is no evidence for the apertural detail shown.

Material. Holotype OSU 19895, Orton Museum of Geology, Ohio State University.

Occurrence. Hyde (1953, p. 336) discovered this specimen in Bed 1, Byer Member of the Logan Formation (Kinderhookian, lower Mississippian, Collins 1979), near Sciotoville, Scioto County, Ohio.

Acknowledgements. J. M. M. thanks the Smithsonian Institution for the Postdoctoral Fellowship which allowed me to undertake this project, and for continued support after my term as a Fellow was completed. R. E. Grant, E. L. Yochelson, T. J. Frest, B. F. Glenister and R. Diecchio kindly read early and later drafts of the manuscript. We are grateful to the Orton Museum of Geology and the University of Cincinnati Geology Museum for their generous loan of specimens. Amoco Research and Production Company defrayed field expenses for S.S. The National Geographic Society kindly provided financial support (Grant 3479–86) which allowed J. M. M. to visit type localities for some of the species described herein. We thank L. Agramonte for her cheerful assistance in the field at Walcott's Secret Canyon locality in Nevada. We are especially grateful to A. J. Gerk for graciously allowing access to his private collection of hyoliths from the Humbolt Oolite.

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Typescript received 26 January 1989
Revised typescript received 20 July 1989